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Longitudinal patterns of dissolved organic carbon concentration and suspended bacterial density along a blackwater river

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Abstract. Dissolved organic carbon (DOC) is the dominant form of carbon in transport in blackwater rivers, and bacteria are the major biological agents of its utilization. This study describes longitudinal patterns in DOC concentration and relates them to suspended bacterial populations in the channel. Concentrations of total DOC, three molecular weight fractions, and bacterial numbers were determined at 12 sites along the Ogeechee River in 1985–86 and 1989 during periods of low and high discharge. Suspended bacterial populations were compared with DOC concentrations to determine if differences in bacterial abundance were related to longitudinal patterns of DOC concentration. Three distinct longitudinal patterns were observed: (1) The longitudinal pattern followed by both total and intermediate molecular weight DOC concentrations was a linear function of the geographic distance along the river. (2) During low flow conditions, there was a high degree of correspondence between patterns of bacterial numbers and low MW DOC (< 1000 apparent MW). (3) During periods of high discharge, the proportion of high (> 10,000) and intermediate (1000–10,000) MW fractions increased, and there was no longer a clear relationship between bacterial cells and low MW DOC.

Introduction

Blackwater rivers are characterized by high concentrations of soluble organic matter. The dominant dissolved organic components in these ecosystems are fulvic acids (Beck et al. 1974), which impart a tea-color to the water. Dissolved organic carbon (DOC) contributes significantly to the pool of organic matter in transport in both clear and blackwater streams; e.g. more than 80% of organic carbon export in two small headwater watersheds was in the dissolved fraction (Hobbie & Likens 1973). DOC represents an even greater percentage of carbon in transport in blackwater rivers. In the Ogeechee River in Georgia, for example, DOC is > 96% of total organic carbon in transport (Benke & Meyer 1988). A common feature of blackwater rivers in the southeastern United States is their low-gradient (little change in elevation per unit river length) that makes viable these rivers show high densities of suspended bacterial populations (0.08 to 1.10×10^{11} cells/L, Edwards 1987), and compared with other aquatic systems, surficial sediment bacterial concentrations are relatively low (0.02 to 5.0×10^{10} cells/g dry wt., Edwards et al. 1990).

Clarifying the pathways and mechanisms for cycling these large pools of DOC is essential to our understanding of aquatic ecosystems because DOC can be an important energy source (Dahm 1981; Meyer et al. 1988). Although DOC is incompletely characterized either with respect to its chemical composition or its availability to bacteria, it plays an important role in physical-chemical processes of adsorption and flocculation (Moore et al. 1979; Lock & Ford 1985). Bacteria play a key role in nutrient cycling and catabolic activity in aquatic ecosystems (e.g. Pomeroy 1974); hence the study of DOC dynamics in rivers is of essential importance in evaluating its possible role in freshwater microbial foods webs (Meyer 1990a).

Variations in the concentration of DOC along a river gradient could be a consequence of a number of factors, including uptake by bacterial populations (Meyer 1986, 1990b), hydrologic regime (Kaplan et al. 1980), or morphological features of the basin (Moeller et al. 1979). Some of these patterns of DOC change along a river were postulated in the River Continuum Concept (Vannote et al. 1980).

The objective of this study was to describe and compare the longitudinal patterns of DOC concentration and suspended bacterial population density along a blackwater river during low and high discharge periods with emphasis on the relationship between bacterial abundance and labile forms of DOC along the river gradient. DOC lability was assessed by characterizing apparent molecular weight of DOC components using ultrafiltration. In previous works, values of apparent molecular weight were correlated with availability of DOC to bacteria in laboratory experiments (Kaplan & Bott 1983; Ford & Lock 1985; Meyer et al. 1987). In this work, the study of variations in the DOC concentration along the river have been useful to look for a relationship between longitudinal patterns of suspended bacterial density and the different DOC molecular weight fractions.

Materials and methods

Study area

The study was carried out on the Ogeechee River, a sixth order blackwater river that drains an area of 13,500 km^2. It flows for about 400 km from its source (at 200 m above see level in the Piedmont Plateau in northeastern Georgia USA) to its mouth, 20 km south of Savannah, Georgia. It has an average annual discharge at the mouth of 115 m^3/s and an average river gradient of $<0.05\%$. The river is not affected by major pollution sources or other anthropogenic perturbations. Agriculture (about 25% of the drainage area) and silviculture are the major forms of land use in a predominantly rural basin in which only about 170,000 people live (Hodler & Shretter 1986).

With the exception of one small portion situated in the Piedmont physiographic region, the drainage basin of the Ogeechee River is in the Coastal Plain (Table 1). The latter region is commonly divided into two physiographic areas: the Upper Coastal Plain characterized by well-drained sandy soils and highly developed dendritic stream patterns with narrow floodplains; and the Lower Coastal Plain which is flatter, has more poorly drained soils and an extensive floodplain that varies from 1 to 2 km in width. In this section, the width of the Ogeechee River floodplain is about 40 times channel width (Benke & Meyer 1988).

The floodplain is covered with a productive mixed-hardwood forest (*Taxodium distichum, Linquidamber styraciflua, Quercus laurifolai, Nyssa sylvatica, Salix* spp.; Pulliam 1991) that contributes large quantities of organic matter to the river during flood periods (annual average litterfall ranges from 716 to 900 g AFDW/m^2; Cuffney 1988). Floodplain inundation occurs as discharge increases. At the most downstream site sampled, inundation begins at 10 m^3/s, but is not complete until discharge exceeds 125 m^3/s. At lower discharges floodplains serve primarily as storage reservoirs of water (Benke & Meyer 1988).

Soils of the watershed are sandy, and the river flows over a shifting sand bottom. Large woody debris is abundant within the channel and provides the only solid substrate in the river (Wallace & Benke 1984; Benke & Wallace 1990). Waters are high in DOC with an annual average of 12.7 mg C/l in the main channel in the Lower Coastal Plain (Meyer 1986). DOC leaches from productive floodplain swamps, because of the low capacity of sandy soils to sorb DOC (St. John & Anderson 1982). Respiration exceeds photosynthesis throughout the year, and appears to be supported by inputs of organic matter from floodplain swamps (Edwards & Meyer 1987; Meyer & Edwards 1990). There is an abundant bacterial

Table 1. Main physiographical features of the Ogeechee River watershed.

Sampling sites	Location	Distance mouth (km)	Stream order	Elevation m (a.s.l)	Physiographic patterns
1	Mitchell	260.5	5	88.35	*Piedmont Region*: (Precambrian). Well-drained sandy soils. Area largely covered by sparce forest. Low wetland areas (small ponds). Gradient 0.08%.
2	Grange	240.5	5	73.12	*Upper Coastal Plain*: (Eocene-Paleocene). Well-drained sandy-clay soils. High fertilized soils. Intensive agriculture: corns, peanuts, soybeans, small grains, cotton . . . Low-medium population density. Narrow floodplains. Average medium-low gradient: 0.046%.
3	Louisville	229.2	5	67.03	
4	Wadley	211.8	6	57.89	
5	Midville	200.5	6	54.84	
6	Millen	171.8	6	39.60	
7	Rockyford	149.2	6	33.51	*Lower Coastal Plain*: (Quaternary). Poorly-drained sandy-loam soils. Soils with a high watertable. High timber harvesting and pastures. Very low population density. Extensive floodplains. Very low average gradient: 0.03%.
8	Dover	140.5	6	27.42	
9	Oliver	113.0	6	19.80	
10	Guyton	83.0	6	10.66	
11	Eden	70.5	6	6.10	
12	'Hilton'	63.0	6	3.50	Drainage area: 6860 km^2. Mean annual discharge: 66.7 m^3/s.

population in the water column, with an annual average standing stock of 3.2 g bacterial C/m^2 at a site in the Lower Coastal Plain (Edwards et al. 1990). Therefore, in this river, processes such as suspended microbial uptake of DOC are potentially important (Meyer 1990a).

Field samples

Streamwater samples were collected on ten occasions at 12 sites along the river (Fig. 1) during 1984—1986 (30 September 85, 18 February 86, 7 August 86, 8 September 86) and 1989 (5 April, 30 May, 21 June, 13

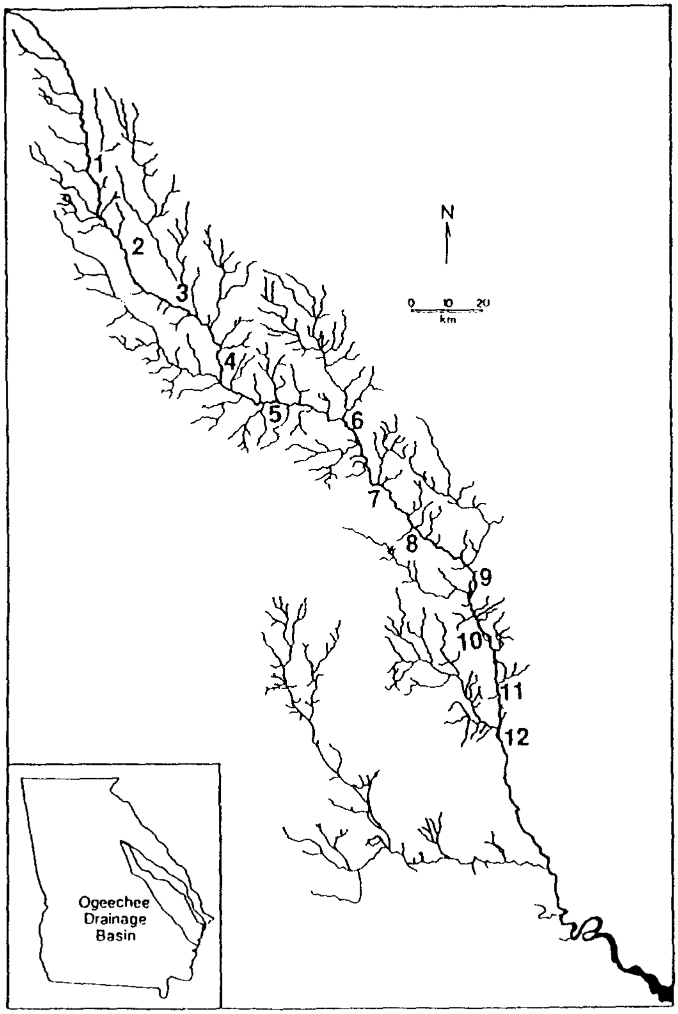

Fig. 1. Map of drainage basin of the Ogeechee River showing the location of sampling sites in the main channel.

July, 1 August, 21 August), coinciding with periods of low and high discharge (Fig. 2). Sampling effort was concentrated at summer and low flow conditions because we hypothesized that under these conditions (high temperature and low discharge) microbiological activity occurring in the river channel would exert its greatest influence on transported DOC.

For DOC samples three replicate water samples were taken in the main channel and filtered through precombusted Gelman AE glass fiber filters

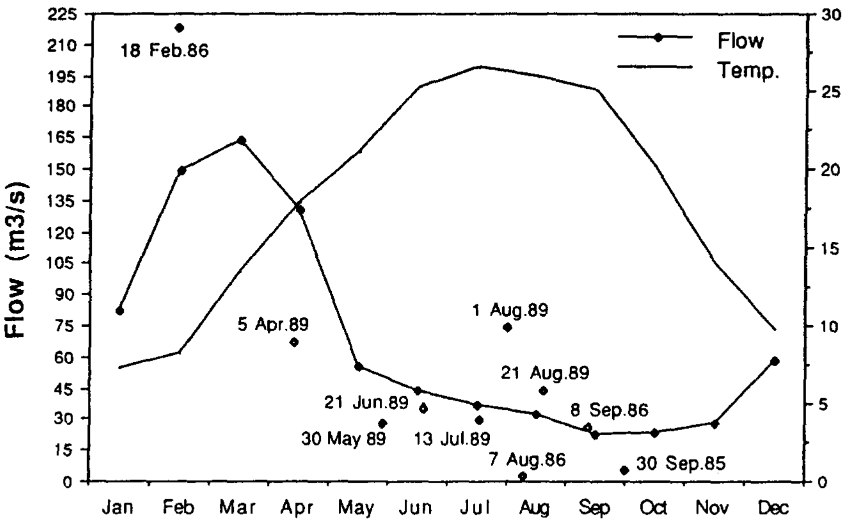

Fig. 2. Annual patterns of discharge (solid line) and temperature (dashed line) in the Ogeechee River. The line indicates mean monthly data for the period 1973—86 from the U.S.G.S. gauging station at Eden (sampling site 11). Discharge values for each sampling date are indicated by individual points on the figure.

(0.3 μm nominal pore size). This filtered water was then separated into different apparent molecular weight (MW) fractions by ultrafiltration through Amicon membranes that had been soaked in 0.2M NaCl overnight and copiously rinsed with deionized water. An Amicon PM 10 membrane was used to separate DOC with MW $<10{,}000$, and an Amicon YM2 membrane was used to separate DOC with MW $<1{,}000$. The different subsamples obtained by ultrafiltration were comparable because pH and ionic strength were constant for each sample. All DOC concentrations were measured on a Dohrman DC-54 carbon analyzer, which uses UV catalyzed oxidation in the presence of persulfate.

The procedure used to estimate MW of DOC really gives measures of molecular size, and the MW fractions obtained by this method are influenced by the nature of the substances being filtered. In particular, the formation of metal-organic matter complexes may alter the apparent molecular size (for example, colloidal iron associated with DOC) (Moore et al. 1979).

Concurrent with DOC sampling, triplicate water samples were taken for bacterial enumeration and preserved in 2% buffered formalin. Numbers of bacteria (rods and cocci) were determined by acridine orange epifluorescent direct counting on black membranes filters (0.2 μm Nuclepore) (Hobbie et al. 1977). Cell volumes were measured (Edwards 1987) and converted to carbon content using a conversion factor of 2.2×10^{-13} g C/μm^3 (Bratbak 1985).

The different variables analysed (DOC fractions and bacterial counts) were subjected to one-way analysis of variance to test whether they changed significantly along the river.

Procedure to describe and compare longitudinal patterns along a river continuum

Several authors have emphasized that longitudinal organization in a stream ecosystem is affected by a gradient of environmental variables; this spatial organization is an important feature of a river (Vannote et al. 1980), which can be described by a series of variables analyzed along the longitudinal gradient. In order to define a gradient of environmental variables, one needs to know the general trend of the variables studied (Fig. 3) and then standardize values among different variables for comparison because they have different units and ranges. One way to do so is to give them the same range, e.g. 0 to 1. The procedure used in this study is the same used by Sabater et al. (1989) in order to detect discontinuities

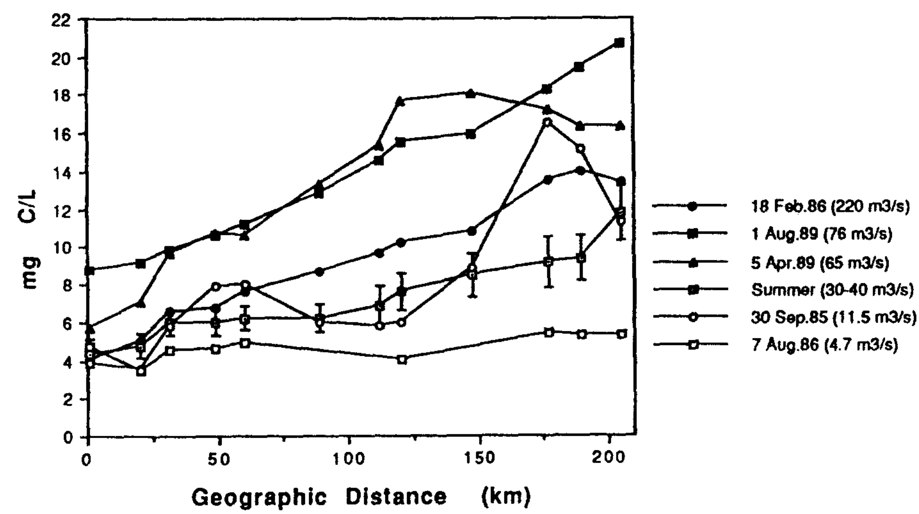

Fig. 3. Total dissolved organic carbon concentrations in mg/L for each sampling date. River discharge is also indicated (data from U.S.G.S. at sampling site 11). Values for the summer period under similar conditions of low discharge and high temperature (8 Sep. 1986, and 30 May, 21 Jun., 13 Jul. and 21 Aug. 1989) are averaged together (mean ± SE).

along another river:

$$P'_i = (P_i - P_{min})/(P_{max} - P_{min}) \tag{1}$$

where P_{max} and P_{min} are the maximum and minimum values of a given variable (P) along the river, and P'_i is the value of the transformed variable at site i. This transformation weights all variables equally and maintains the proportional difference in P between two sampled sites (X_i to X_j) along the continuum:

$$dP'_{ij} = P'_i - P'_j = dP_{ij}/(P_{max} - P_{min}). \tag{2}$$

According to this procedure, each calculated difference can be considered as a measurement of the change in a given variable (P) between two points (i, j) (i.e. inter-site differences for each transformed variable). When this change is related to the geographic displacement (dX'_{ij}) which is also calculated by equation (2) where X is km from the source), different slopes for each stretch of the river are obtained (dP'_{ij}/dX'_{ij}). The slope is the rate of change of that variable over that stretch of the river.

A graph of variables transformed using equation (1) versus geographic distance along the river channel [also transformed using equation (1)] describes each variable's overall longitudinal pattern, which can then be defined by an empirical equation. A pattern described by a linear equation implies a constant rate of change along the river, i.e. that the variable is affected by processes that vary proportionally with distance along the channel (e.g. constant biological production or uptake per linear distance of channel), whereas a positive exponential pattern implies constantly increasing rate of change along the channel (e.g. increasing inputs per linear distance of channel). Hence a change in pattern type suggests a shift has occurred in the river, and an erratic pattern suggests discontinuities that could have been produced by disturbances.

Results

Patterns in DOC concentration along the Ogeechee River

Total DOC concentration significantly increased downstream on all dates ($p < 0.05$). However, the range of concentrations was quite different on different dates (Fig. 3) except during summer 1989, when samples from all four dates with low discharge and high temperature had similar values. Hence these summer 1989 dates were combined and a mean value for each site plotted in Fig. 3. Highest DOC concentrations were observed when the river was flooded and the lowest when discharge was low. In a previous study in this river, Meyer (1986) also found a direct relationship between total DOC concentration and stream discharge at site 12, with summer storms exhibiting the highest DOC concentrations.

The intermediate molecular weight (1,000—10,000 MW) fraction is the size of fulvic acids (Meyer 1986) and was always the dominant DOC fraction at all sites (Fig. 4); this had also been observed previously at a single site (Meyer 1986). This fraction tends to increase downstream and was usually responsible for most of the increase observed in total DOC (Fig. 3). The other two fractions (< 1,000 MW and > 10,000 MW) did not consistently increase downstream (Fig. 4).

To ascertain longitudinal patterns of DOC for each sampling period, we transformed all DOC parameters and geographical real distance using equation (1). We then graphed these transformed variables for different

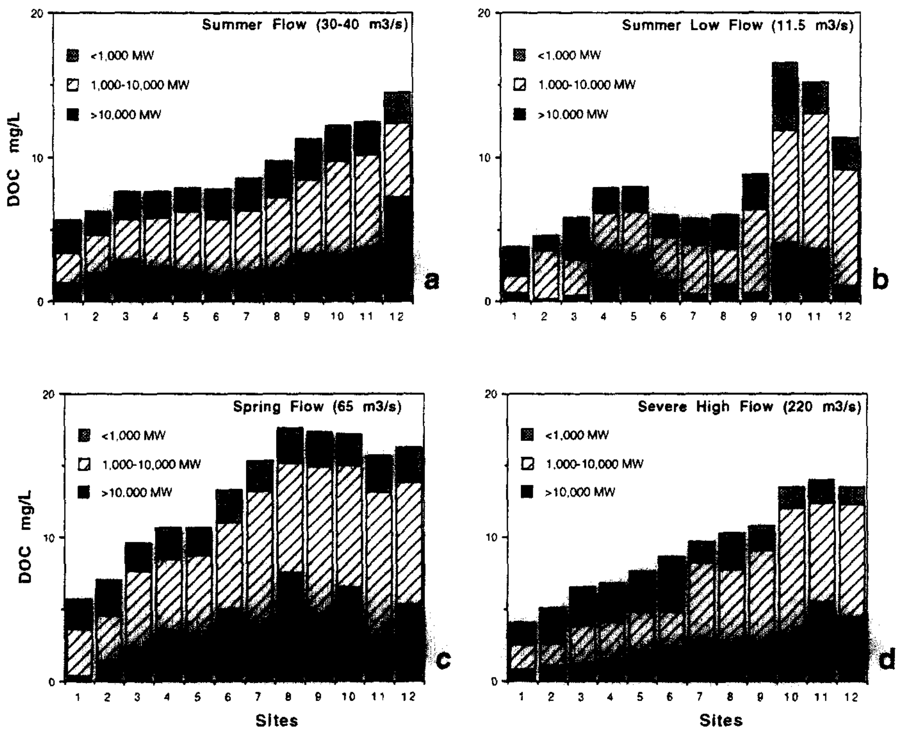

Fig. 4. Proportions of DOC molecular weight fractions at each sampling site along the Ogeechee River at different flow conditions: a. Average concentrations under similar discharge during summer (30—40 m^3/s at site 11). b. Summer low discharge (11.5 m^3/s). c. Spring discharge (65 m^3/s). d. Extremely high flow in winter (220 m^3/s).

dates and fit empirical equations. Under similar conditions of discharge and temperature, there was a consistent longitudinal pattern for all DOC values. Therefore, we clustered data from sampling periods (8 Sept. 86, 30 May 89, 21 June 89, 13 July 89, 21 Aug. 89) with similar discharge (between 30 and 40 m^3/s) and temperature (about 25 °C), describing a unique longitudinal pattern for total DOC and each fraction under these summer conditions (Figs. 5, 6 and 7).

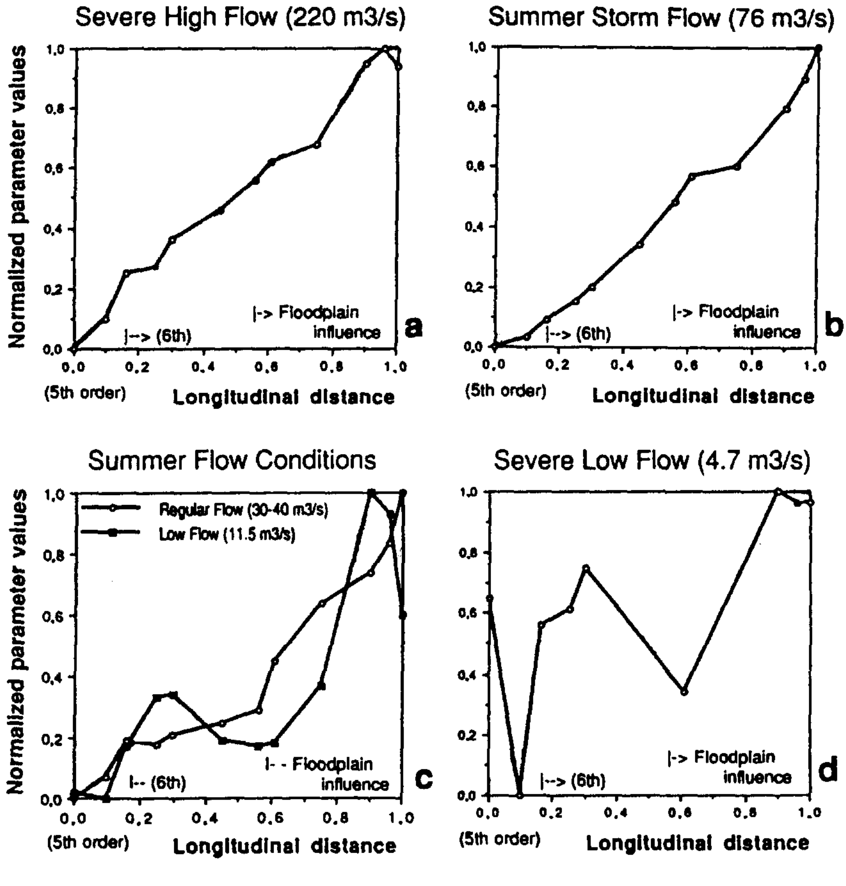

Fig. 5. Longitudinal patterns of total DOC along the river continuum under different discharge conditions. Total DOC values have been transformed and related to the distance between sampling sites (see text). a. Very high flow. b. Summer storm flow. c. Similar summer conditions (low flow and high temperature). d. Very low discharge. A linear function means a proportional variation in DOC content along the river, whereas a positive exponential pattern (Fig. c) indicates a progressive increasing rate of change of DOC indicating a strong floodplain influence on the channel. The erratic pattern shown in Fig. d suggests discontinuities that could have been produced by disturbances. The stream order at the site and the part of the river in the Lower Coastal Plain with greater floodplain influence are indicated on the figures.

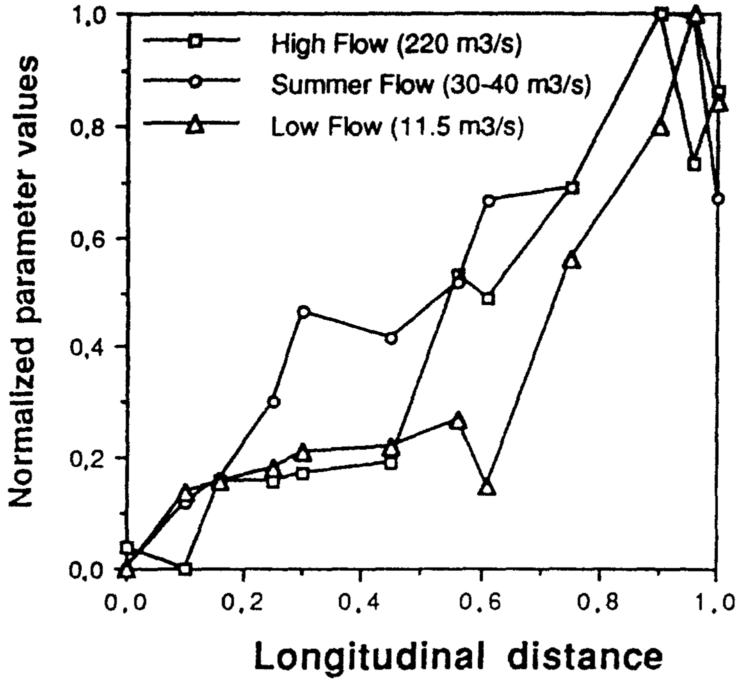

Fig. 6. Longitudinal patterns of the intermediate molecular weight fraction (1,000—10,000 MW) under three different discharge conditions. The data are fit by the following three equations (lines for these equations are not shown): for high flow, y = −0.05 + 0.94 x (r^2 = 0.91, p < 0.001); for summer flow, y = 0.06 + 0.87 x (r^2 = 0.88, p < 0.001); for low flow, y = 0.09 $e^{2.12x}$ (r^2 = 0.91, p < 0.001).

At extremely high flow conditions (220 m^3/s, on 18 Feb. 86) and during a summer storm (76 m^3/s on 1 Aug. 89), the longitudinal pattern for total DOC is described by a linear function with a slope of 0.96 (r^2 = 0.98; p < 0.001) and 0.99 (r^2 = 0.98; p < 0.001) respectively (Fig. 5a, b). However, during lower summer discharge (Fig. 5c), longitudinal patterns were described by exponential equations: at a flow of 11.5 m^3/s, the equation is y = 0.04 $e^{2.96x}$ (r^2 = 0.65, p < 0.05), and at flows between 30—40 m^3/s, y = 0.08 $e^{2.42x}$ (r^2 = 0.92, p < 0.001). Under extremely low flow conditions (4.7 m^3/s on 7 Aug. 86) (Fig. 5d), the pattern was extremely irregular indicating high-spatial variability that could reflect high variability in DOC concentration of water entering from the floodplains or localized sites of high biological activity.

Intermediate MW compounds (1,000—10,000 MW) are considered the most refractory (Meyer et al. 1987) and showed a linear increase downstream at all except the lowest flow conditions. At low flow conditions, its

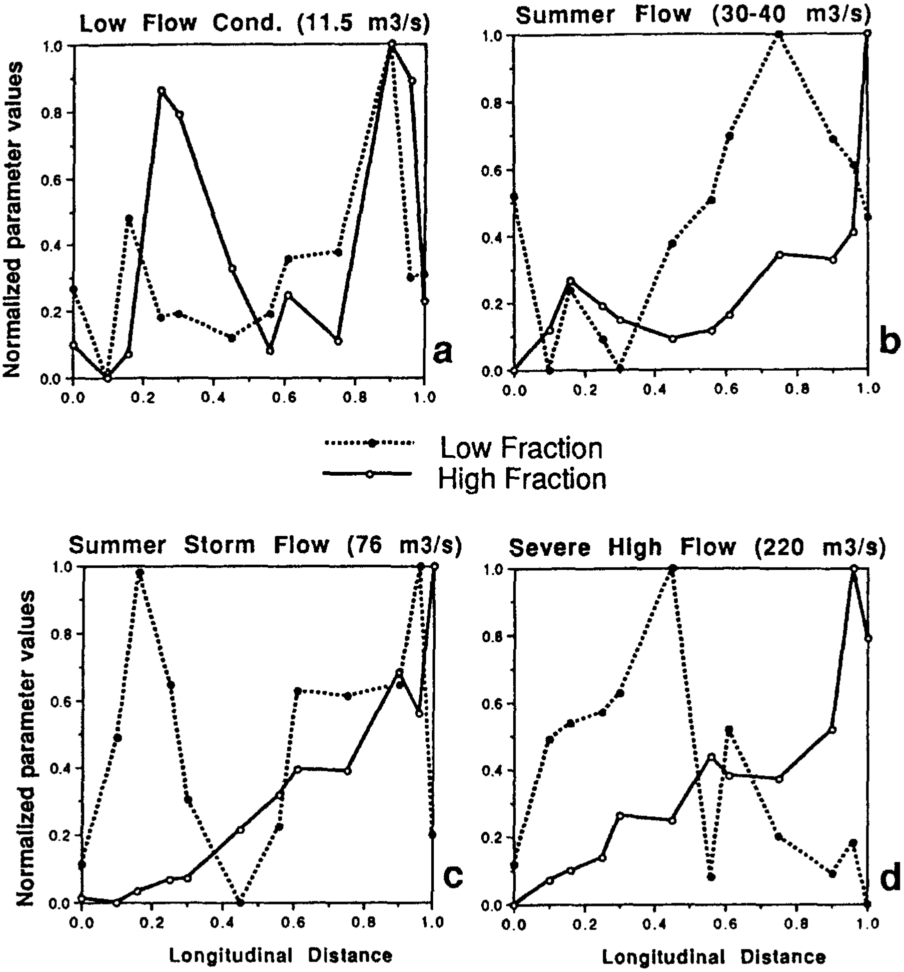

Fig. 7. Comparison between longitudinal patterns of low (<1,000 MW) and high (>10,000 MW) DOC fractions during different discharges: a. Low discharge (11.5 m^3/s at site 11). b. Average summer flow (30—40 m^3/s). c. Summer spate (76 m^3/s). d. Severe high flow (220 m^3/s).

longitudinal pattern can be described by an exponential equation, because it fits significantly better than a linear equation. Longitudinal gradients of the other two fractions differed with flow. Transformed values of these two variables were significantly correlated ($p < 0.05$) during very low discharge (11.5 m^3/s on 30 Sept. 85, Fig. 7a), but were not correlated at higher flow conditions (Fig. 7b, c, d). The patterns of the high MW fraction during summer storm flow (76 m^3/s) and at a very high flow (200 m^3/s) were described by these equations respectively: $y = -0.11 + 0.84\ x$

($r^2 = 0.87$, $p < 0.001$), and $y = -0.03 + 0.78\,x$ ($r^2 = 0.84$, $p < 0.001$). At higher discharges, the longitudinal pattern of the high MW fraction was linear like the intermediate MW refractory compounds (Figs. 7c, d). The fact that intermediate MW DOC (the predominant fraction of DOC, Fig. 4) was most closely correlated with geographic distance, while higher or lower MW fractions were more poorly or not correlated, suggests that this intermediate fraction may be least changed by biological processes along the river. This is supported by the observation that the longitudinal pattern of concentrations of a conservative compound like chloride is also linear, in contrast to compounds like soluble reactive phosphorus or nitrate that are more susceptible to change resulting from biological activity (Fig. 8).

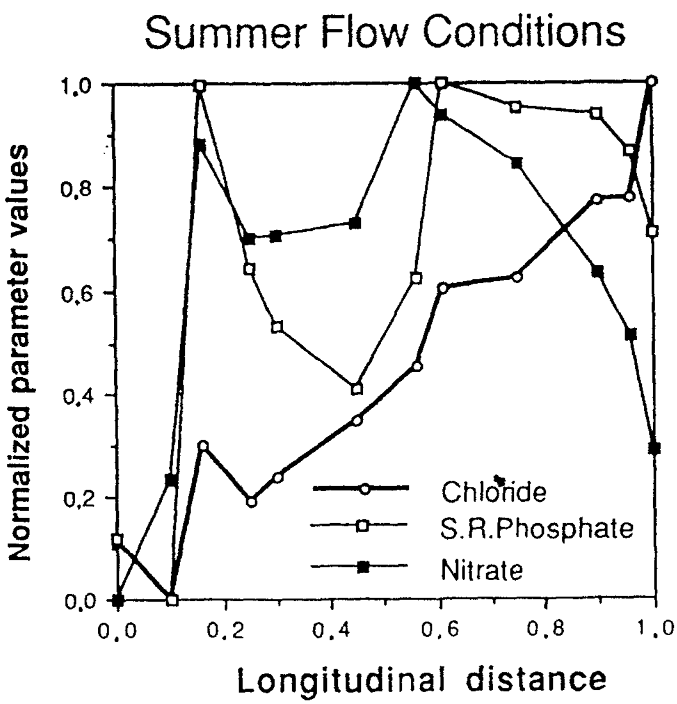

Fig. 8. Difference in longitudinal pattern between a conservative parameter (chloride) and non-conservative parameters (nitrate and soluble reactive phosphorus).

Bacterial population density along the Ogeechee River

The numbers of total bacteria ranged from 0.55 to 1.5×10^{10} cells/L during 1989, while samples from 1985–86 had higher densities (from 0.8 to 11.5×10^{10} cells/L), primarily because much higher discharges were sampled during 1985—86. Generally, bacterial numbers were slightly higher upstream and decreased gradually downstream to the beginning of the major floodplain area. From this point, bacterial densities increased quickly downstream, although the increase differed with the discharge being sampled. Figure 9 plots the longitudinal distribution of mean bacterial density along the river during 1989. Sampling points with the highest standard error values coincide with regions of major floodplain influence. This high fluctuation suggests that floodplains are a source of allochthonous bacteria and perhaps also a source of growth substrate for bacteria. Standard errors at these sites are reduced when one compares sampling dates with similar discharge and temperature conditions.

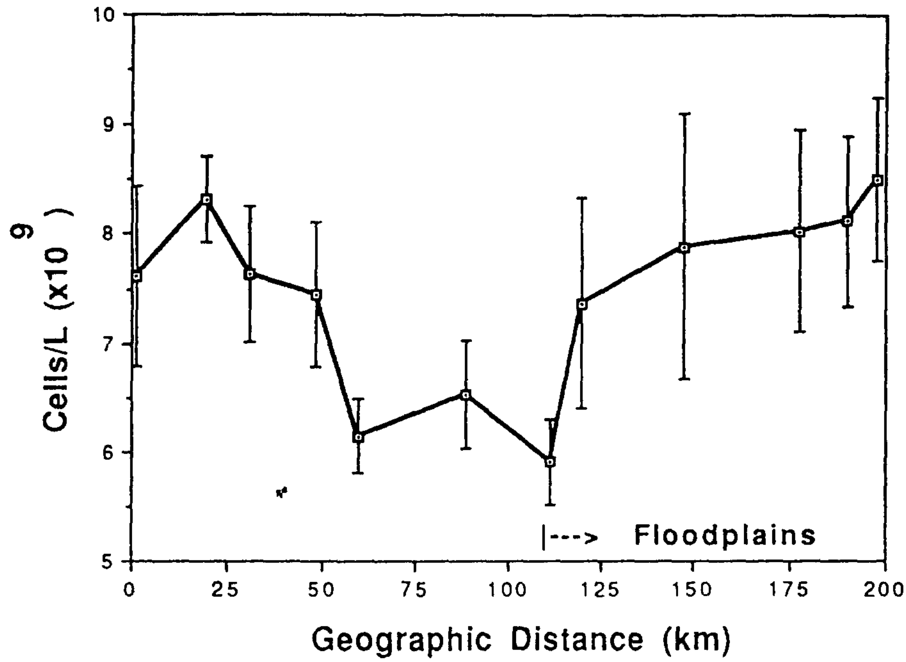

Fig. 9. Mean (±SE) values of total bacterial cells/L along the Ogeechee River from all 1989 dates sampled. Distance along the river is measured from first sampling point, not from the source.

Edwards (1987) found that cell densities at site 12 were greatest during high water conditions in winter and lowest during low water periods in summer. However, we did not find good correlations between bacteria and discharge in this study, probably because we sampled a more limited range of discharges, and most of the samples were taken under lower discharge conditions. Low values for bacterial numbers occurred during both high and low flow conditions. On dates sampled during 1989 (when the floodplain was never totally inundated; Pulliam 1991), the highest cell numbers and biomass were found during summer. Servais (1989) also found higher levels of biomass and bacterial production during summer than winter conditions and an increase in bacterial biomass and production from upstream to downstream along the Meuse River in Belgium.

Comparing longitudinal patterns of DOC and suspended bacteria along the Ogeechee River

Low MW fractions of DOC are more readily utilized by bacteria; uptake of high MW fractions occurs at a slower rate and is sometimes inhibitory to utilization of other fractions (e.g. Kaplan & Bott 1983; Ford & Lock 1985; Meyer et al. 1987; Freeman & Lock 1992). Therefore in this study we compared patterns of bacterial abundance and low MW DOC concentration. We found a high degree of correspondence between transformed values for low MW DOC and bacterial numbers or biomass during periods of low discharge and high temperature (Fig. 10a, b); these correspondence was much less evident at higher discharges (Fig. 10c, d, e).

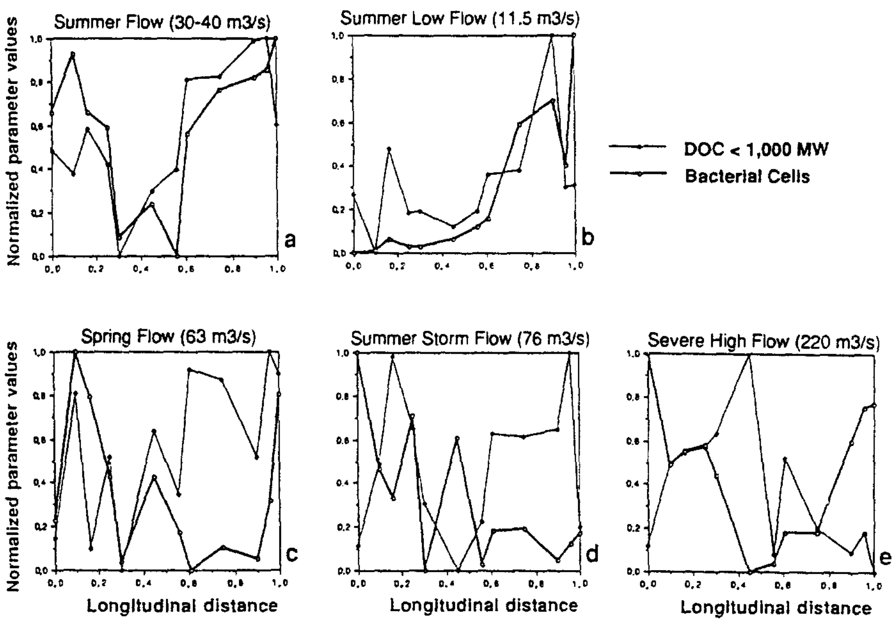

Fig. 10. Relationships between longitudinal patterns of low MW DOC fractions and bacterial density under different flow conditions: a. During similar summer flow (30–40 m^3/s at site 11). b. At low flow conditions (11.5 m^3/s). c. During spring flow (63 m^3/s). d. During summer spate (76 m^3/s). e. During very high discharge (220 m^3/s).

These patterns suggest that at low discharge bacterial populations are responding to increasing amounts of low MW DOC coming from the floodplains (Fig. 7). The impact of low MW DOC on bacterial biomass is clearly affected by hydrologic conditions, since patterns break down during periods of high discharge.

Discussion

It is not possible at present to identify all of the individual organic compounds which comprise DOC, although it is well-known that within the DOC pool some compounds and MW fractions are more biologically and chemically labile than others (Wetzel & Manny 1972; Ladd et al. 1982; Meyer et al. 1987). Compounds which form biologically recalcitrant complexes often increase in concentration with distance downstream (Kaplan et al. 1980; Wallace et al. 1982; Ford & Lock 1985; Meyer & Tate 1983), and the relative availability of DOC to bacteria decreases along the Ogeechee River continuum (Leff & Meyer 1991). One might expect that much of the labile DOC is rapidly removed, leaving the refractory compounds to be transported downstream (Wetzel & Manny 1972). One would then expect intermediate and high MW DOC to show a more linear longitudinal pattern than labile compounds, which is what we observed. Although the pathways and mechanisms for cycling pools of DOC are numerous, microbial uptake appears to be a significant biotic mechanism for DOC removal from the water column in blackwater rivers (Meyer 1986).

Longitudinal patterns of bacterial numbers and DOC in the Ogeechee River illustrate the influence of hydrologic exchanges on within-channel processes in a river with an intact floodplain. If bacterial growth is supported by utilization of DOC, one might expect DOC concentrations to decrease as bacterial population increase. However, if most DOC is not utilized by bacteria, either because it is not available or because uptake is too slow relative to travel time along the river, then we would expect similar longitudinal patterns of bacterial populations and DOC concentration. Both conditions apply here: during 3-day laboratory growth experiments, little growth of Ogeechee River bacteria was observed on intermediate MW DOC, which comprised the bulk of DOC, and bacteria utilized 54% of low MW DOC (Meyer et al. 1987). The high degree of correspondence between low MW DOC and bacterial numbers during summer low discharges observed in this study supports the idea that concentrations of low MW DOC influence bacterial abundance. A similar relationship was observed in a Welsh stream over an annual period (Ford

& Lock 1985). It is also possible, although less likely, that both bacteria and low MW DOC are being supplied from the same source, resulting in similar longitudinal patterns. At low discharges that source is not likely the floodplain or groundwater, which has very low DOC concentrations (R. T. Edwards, unpublished data). Although bacteria may be coming from the river sediments, it is difficult to imagine sediments providing a large source of low MW DOC. During high discharges unclear relationship between low MW DOC and bacteria trends was found, suggesting that channel processes are overloaded by inputs of allochthonous bacteria and DOC from surrounding swamps. Flooding would cause variable runoff from different expanding low-lying areas, bringing allochthonous populations of bacteria (presumably with low viability) and heterogeneous (including some more refractory) sources of organic matter into the river channel. Evidence from the Ogeechee River suggests that DOC during floods is less available to bacteria: using a direct measure of DOC availability to native bacterial populations, Leff & Meyer (1991) observed less bacterial carbon produced per mg DOC present at high discharge than at low discharge.

In addition to biotic uptake, physical-chemical mechanisms for DOC uptake can also influence longitudinal patterns of DOC concentration. These processes include sediment adsorption, flocculation, photochemical destruction, hydrolysis, and metal chelation by amorphous solid phases of aluminium and iron oxides (Moore et al. 1979). Photochemical oxidation does not appear to be a major pathway for DOC removal in the Ogeechee River (Meyer 1986). Other abiotic pathways may be more important, particularly for the higher MW fractions. Microcosm studies using Ogeechee River water have shown that formation of particles from DOC can occur in the absence of microbial activity (Carlough 1989).

Allochthonous input from surrounding terrestrial ecosystems (e.g. McDowell & Likens 1988) and autochthonous input both may be sources of DOC in stream ecosystems (Kaplan & Bott 1982; Ladd et al. 1982). However, the organic matter in this blackwater river is derived mainly from allochthonous sources, primarily floodplain swamps. Over a two year period, the Ogeechee River floodplains exported 9.8×10^7 kg C (Cuffney 1988). More than 70% of DOC inputs to undisturbed streams are considered refractory to rapid microbial degradation (Wetzel & Manny 1977). Otherwise, if the time required to remove any class of molecules from the DOC pool exceeds the residence time of the molecules in the reach, and if there are additional high-concentration inputs of DOC from floodplains, concentrations of total DOC should increase downstream. This is what we have found in this study, although previous reports of increases in DOC concentration downstream have been limited to headwaters of stream systems (Kaplan et al. 1980; Johnson et al. 1981; Wallace et al. 1982; Meyer & Tate 1983; Meyer 1990b). During both rising and high water in the Amazon River, DOC concentration was relatively uniform throughout the river, with some elevation below its confluence with the blackwater Rio Negro (Ertel et al. 1986). Moeller et al. (1979) report only minor changes in DOC content in two large rivers (seventh-order); and Malcolm & Durum (1976) did not find significant increases of DOC from headwaters to estuaries, although both of the studies involved higher-gradient rivers with little floodplain interaction. There was no consistent trend in DOC concentration in a Quebec blackwater river (Naiman 1982); but this also is a river with narrow floodplains. A downstream increase in DOC concentration is a characteristic of the blackwater river we have studied. This pattern may be a consistent feature of rivers characterized by extensive floodplains.

Conclusions

Almost all the increase in total DOC concentration observed along the Ogeechee River is a consequence of high concentrations of high (> 10,000 MW) and intermediate (1,000–10,000 MW) MW fractions downstream. This is probably the net result of two processes: more rapid uptake of low MW fractions (labile compounds; Meyer 1986), and leaching of refractory and high MW components into the channel from the floodplain. Neither the longitudinal pattern of the highest MW fraction of DOC nor its intermediate fraction has a clear relationship with bacterial cell distribution along the river.

Our data have revealed two distinct longitudinal patterns which result from the interaction of floodplains and biotic and hydrological processes. During flooded conditions, longitudinal patterns of bacterial populations and total DOC or any MW fractions did not show any clear relationship. DOC content along the river appeared to be affected by high runoff from the floodplain. Its increase and accumulation in transport is a conspicuous feature of these flow conditions. The second pattern was observed under summer low-flow conditions. DOC inputs from floodplains were minimal, and the longitudinal patterns followed either by bacterial density or by bacterial biomass showed a high degree of correspondence with low MW DOC. Under these conditions, the longitudinal pattern of suspended bacteria in the main channel appears to be affected by the distribution of labile DOC compounds along the Ogeechee River.

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